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Evolution of Play

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Synonyms

Adaptive play behavior; Phylogeny of play behavior; Play as adaptation

Definition

Play behavior can be studied as an adaptation evolved to develop motor and problem-solving skills, assess one's own capabilities in relation to one's environment, and learn how to interact and perhaps cooperate with social partners; play can also be considered phylogenetically as a trait that has evolved divergently, convergently, and in parallel.

Introduction

Play behavior is highly prevalent across much of the animal kingdom, especially in the mammalian lineages. This prevalence suggests that play behavior must be an evolved adaptation, but developing and testing hypotheses to explain its origins has proved challenging. Understanding play behavior from an evolutionary perspective requires that play be clearly defined, that we have clear hypotheses explaining the relative costs and benefits of play, and that these adaptive hypotheses can be tested through direct or indirect observation. This entry explores how ethologists have observed and defined play in a variety of animal species (including humans) and how play has been explained from an evolutionary perspective. The evolution of play has been investigated through the methods of ethology and phylogenetics, both of which will be reviewed here. As the most playful species on the planet, humans have much to learn from studying both human and nonhuman play from an evolutionary perspective.

Why Play?

To evolve, play behavior must be adaptive. By definition, a behavior is an adaptation if it increases an individual's chances of surviving and reproducing relative to alternative behavioral options. Playing sometimes seems like a waste of time, or inordinately risky, because play behaviors don't appear to provide immediate benefits: play is frivolous, a luxury. How might play increase the overall prospects for survival and reproduction? What benefits offset the costs of play, and when/how do these benefits appear? How have organisms evolved to respond to particular environmental conditions by playing? How is play related to development and the attainment of reproductive

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maturity? Why are some species prolific players, while others do not play at all? Understanding play from a Darwinian perspective requires that we address these questions.

Costs of play. Play is a behavior with clear potential costs. There is an opportunity cost associated with play behavior, as it produces no immediate benefits: time spent playing could be spent resting, searching for a mate, or finding resources. Many forms of play are physically demanding and therefore come with an energetic cost. Because play is immersive and often occurs in open spaces, it can leave individuals more exposed to predators. Many forms of play involve risk-taking, making injury a potential cost as well. The fact that there are so many measurable risks of play behavior makes it all the more important to establish what benefits have driven the evolution of play.

Play as an evolutionary paradox. Play is an apparent paradox because it appears, on first assessment, to be a wasteful behavior. Why would an animal expend energy, exclude itself from more immediately productive activities, and expose itself to increased risk if playing provides no direct or immediate benefits? So long as the benefits of play remain unquantified, play appears to be an evolutionary paradox. This paradox can be resolved if play behaviors lead to indirect or delayed benefits that are large enough to offset the immediate costs of playing. Since one of the defining characteristics of play is that it has little immediate function, it is a given that benefits must be measured after play has occurred; how long it takes for these benefits to be manifested depends on the life history of the animal as well as the kind of play that that animal engages in.

Benefits of play. Numerous benefits of play have been suggested, but most fit into one of six broad categories. Play can be used to:

1. Develop motor skills
2. Train for the unexpected
3. Assess one's own physical and cognitive capabilities
4. Assess the reliability and capabilities of potential social partners
5. Learn social norms
6. Foster social cohesion

Many animal species maintain plastic neurological systems that allow for the development of motor skills through the practice that play can provide; such developmental employment of play is particularly common in juveniles. Whereas developing motor skills involves training for normal or expected behavioral responses, it is also possible that the spontaneous and uncontrolled nature of play may train animals to respond to unexpected environmental conditions. Play may be a means by which animals can assess their own capabilities in relation to prey, competitors, or predators; such assessment may enable animals to manage the behavioral balance between risk and reward in varying environments. Play may also be a means of assessing the capabilities of potential social partners; such assessment is crucial for animals which choose to work cooperatively with particular members of their social group. For species whose survival depends on social interactions, play can be a means by which young animals learn the norms that govern those interactions. And in species where social cooperation is important, play can be a means by which individuals form the bonds that create a cohesive social group.

While each of these potential benefits is distinct from the others, particular forms of play can provide more than just one of these benefits. A cat batting around an inanimate object may be both developing better predatory motor skills and gaining an understanding of what sorts of prey it is capable of actually catching. Play-fighting in meerkats may also develop motor skills (most likely to escape predators) but in addition may allow individuals to assess the capabilities of their social partners and create the social cohesion necessary to foster the very extensive cooperation that occurs in meerkat colonies.

It is relatively easy to observe play behavior and hypothesize various benefits it might provide, but testing these hypotheses by observing the increases in fitness they predict is more challenging (Burghardt 2005). Studies of horses (Cameron et al. 2008) and bears (Fagen and Fagen 2004)

have demonstrated that the degree to which animals play as juveniles positively correlates with their prospects for survival to adulthood. Juvenile Belding's ground squirrels that played more often scored higher on tests of motor skills (Nunes et al. 2004). Playing as juveniles increased the resiliency of elephant calves and increased their probability of surviving as adults (Lee and Moss 2014). A study of captive mink showed that increased rough-and-tumble play correlated with optimal adult sexual behaviors in both males and females (Dallaire and Mason 2017). Further study is required to causatively link play behavior to one or more of the benefits outlined above and ultimately to increased probabilities of survival and reproduction.

When play should evolve. Evolutionary theory suggests that play behavior should evolve when the benefits of that behavior exceed its costs, with both costs and benefits measured as changes in the probability of surviving and reproducing. The benefits and costs of play may vary in different environments. In particular, resources may play a role in modulating costs and/or benefits: in a resource-rich environment, the opportunity costs of playing may be reduced, while the potential benefits of playing may increase. For this reason, animal parents may invest in their offspring in ways that optimize the cost-benefit ratio of play (Cameron et al. 2008), allowing play to evolve as a critical component of normal physical and social development.

Hypotheses explaining why play evolves. The potential functional benefits of play imply hypotheses about why play has evolved in various species; nonfunctional hypotheses are also potentially important, especially if play behaviors represent a by-product of other adaptive traits. Spinka et al. (2001) considered their own hypothesis (*training for the unexpected*) alongside three other functional explanations (*motor training*, *self-assessment*, and *surplus energy*) and one by-product explanation (*surplus resources*). They then created a framework for comparing the relative support for each hypothesis by delineating 24 predictions that created strong contrasts between each hypothesis. Interestingly, their framework of comparison did not explicitly address some of the hypothesized social benefits of play (although if conceived broadly, "training for the unexpected" can produce benefits that relate to social norms and cohesion).

Testing the predictions made by different hypotheses. Understanding how play evolved requires that alternative hypotheses make clear predictions and that these predictions be testable. Hypotheses explaining the evolution of play can be applied to specific play behaviors in particular species or to play behavior across the animal kingdom (e.g., Spinka et al. 2001), although the diverse nature of play makes it unlikely that a single hypothesis will explain all instances of play behavior (Burghardt 2014). Even within a particular species, more than one hypothesis may be required to explain the full breadth of play behavior; for example, Sommerville et al. (2017) reviewed the literature on play behavior in domesticated dogs and discovered strong support for the predictions of both the *motor skills development* and *social cohesion* hypotheses. In considering why adult dogs play, Bradshaw et al. (2015) reached a similar conclusion and suggested that different forms of dog play behavior may actually have independent evolutionary origins.

The prospect of studying play from an evolutionary perspective is exciting, as doing so could resolve the apparently paradoxical nature of play. Play does have an ultimate function, even if it seems frivolous at the time. But in order to study play behavior scientifically, we need a clear definition of what kinds of behaviors constitute play. We can roughly identify play by its characteristics: it's fun, it's done for its own sake, and it is done in times and places that feel safe. But actually distinguishing play from non-play behaviors is not so simple and has presented a challenge to scientists who study play.

Defining Play (Is Not So Easy)

What is play? As an extremely playful species, humans ought to be able to identify play when we see it. But play turns out to be very difficult to

precisely define. One reason that play can be difficult to identify is that it takes many forms and can serve many functions, making it a "heterogeneous" behavior requiring a fairly broad definition. Play behavior itself is often separated temporally and spatially from the benefits it can provide, making it more difficult to determine whether an observed behavior should be called "play." Play behaviors are often defined by an affective state ("having fun") which itself is difficult to define (or directly observe). That humans are as a species so playful also complicates our ability to determine what defines play; our tendency to anthropomorphize the behavior of other animals may produce definitions of play that are too inclusive, whereas our tendency to take a very anthropocentric view of our own behaviors can produce definitions of play that are too exclusive. For play to be studied scientifically, a clear definition is required.

Many (conflicting) definitions. Play has been a subject of serious study for well over a century, but researchers examining play have failed to come to consensus on a definition of what constitutes play (Burghardt 2005). There is disagreement over whether play is productive or a waste of time, whether it is pro-social or antisocial, and whether it is safe or dangerous. Some researchers argue that play is not definable and therefore beyond scientific study, whereas others seek to define play as a behavior that can be studied from a Darwinian perspective.

Some of the conflict over how (and whether) to define play emerges from the different approaches of the ethological and psychological sciences. Whereas ethologists rely on clear behavioral distinctions that do not require knowledge of the internal state of the animal performing that behavior, psychological definitions may emphasize the private experience that underlies behavior (Brown 2009).

Burghardt's five criteria. To mitigate some of the confusion over what constitutes play and to advance the study of play from an evolutionary perspective, Burghardt (2005) advanced five criteria to define play behavior. These criteria are briefly summarized as:

1. Limited immediate function
2. Endogenous component
3. Structural or temporal difference
4. Repeated performance
5. Relaxed field

That play behaviors have *limited immediate function* hinges on the idea that the evolved benefits of play are indirect or delayed; although not all behaviors that fail to produce immediate benefits should be considered play, the absence of clear immediate benefits sets up the possibility that a behavior could produce delayed benefits. Behaviors with an *endogenous component* are performed in a manner that is not simply a response to external stimuli; Burghardt defines these behaviors as "spontaneous, voluntary, intentional, pleasurable, rewarding, reinforcing, or autotelic." To display *structural or temporal difference*, a play behavior must differ in some manner from other behaviors that serve a more direct functional purpose; many play behaviors are performed partially, in an exaggerated form, or in different times and places than analogous non-play behaviors. *Repeated performance* implies that during some point in the development of an animal, a particular behavior is practiced, often in a progressively varying manner. Finally, play behaviors are performed in a *relaxed field*, which is to say that animals only play when they are healthy, their basic needs are met, and they are free from stresses such as resource/mating competition or predation risk. A key aspect of Burghardt's five criteria is that they are interactive: while no single criterion sufficiently filters play from non-play behaviors, applying all five criteria can produce a relatively clear distinction.

Categories of play. Ethologists who study play have conceptualized three main categories of play behavior. *Locomotor-rotational play* includes various forms of body movements performed independently by individual animals. *Object play* involves the manipulation of objects found in the environment. *Social play* occurs when two or more animals interact as part of the play behavior.

These categories of play are not mutually exclusive: in fact, it is possible to imagine all

three co-occurring in particular contexts. For example, wild bottlenose dolphins have been observed numerous times surfing waves into the shore, usually independent of feeding or any other behavior with direct function (Paulos et al. 2010). Surfing by dolphins is definitely a form of locomotor-rotational play because it requires that dolphins practice body movements that produce the ability to ride the wave. It could also be a form of object play where the wave itself is the object that is played with. And if dolphins surf together, having to maintain safe distance to avoid collisions with groupmates, then surfing could also be a form of social play.

Many forms of human play also simultaneously encompass all three forms of play. Consider a group of people at the park throwing around a flying plastic disc. This play is most obviously object play, as the players must learn how to throw and catch the disc. But learning how to play with the flying disc also involves locomotor-rotational play, especially in catching errant throws from less experienced players. And as with any game of "catch," playing with a flying disc is an inherently social activity that requires players to empathize with and anticipate the needs of their playmates.

Levels of play. A number of play researchers have suggested that play should be considered along a continuum of hierarchical levels. These include Robert Fagen's five levels of play, which emphasize the complexity of social interaction involved in play, and Robert Mitchell's four levels, which emphasize the degree of simulation and intent involved in a particular form of play (Burghardt 2005). Both of these classification schemes recognize that solitary play differs from play that is done in parallel or direct interaction with other individuals and consider social play to be more sophisticated than solitary play.

Particularly human extensions of animal play. The diversity of human play presents particular challenges to any categorization scheme. In addition to engaging in play behaviors that can be classified as locomotor-rotational, object, or social, humans also engage in forms of play that involve creative exploration, mental simulation, and complex roles. Some of these behaviors differ from other animals in extent, but others appear to differ in kind. It has been argued that many animals maintain rules of play (Bekoff and Pierce 2009), but no other animals play employing the complex rule sets of organized sports or strategy games. While it may be impossible to fully ascertain the degree to which other animals perform mental simulations and pretend, it is clear that human language and – more recently – audio and visual technologies empower unrivaled levels of play that emerges predominantly within our brains. Play is a major source of innovation (Bateson 2014), and it is innovation that drives the human species' unique form of cumulative culture. To more fully encompass the diversity of human play forms, many researchers employ additional categories such as "free," "creative," "narrative," and "reenactment" (Dallaire et al. 2017).

Differentiating play from functional and dysfunctional behaviors. A number of common animal behaviors should not be considered play despite sharing some of the characteristics that typify play. Humans often associate being playful with exploration and pursuits that satisfy our curiosity. While exploratory behaviors motivated by curiosity can be forms of play, it is important to recognize that many forms of exploration produce immediate functional benefits (Burghardt 2005). An animal may intensely examine a new enclosure or novel environment, but such an examination could simply provide valuable information about where to find resources or where to avoid exposure to aggression or predation. For exploration to constitute play, it must be repeated in some manner, provide delayed benefits, and occur in a low-stress environment.

Animals sometimes display behaviors that are maladaptive rather than adaptive and therefore do not constitute play. For this reason, stereotypies such as continual pacing and excessive grooming should not be considered a form of play. That such dysfunctional behaviors have almost exclusively been observed in the radically different environments created by captivity suggests that perhaps stereotypies could result from a mismatch between evolved play responses and

the unnatural environments created for other animals by humans.

Four perspectives on play behavior. As with all forms of animal behavior, it can be useful to consider play behavior from Tinbergen's four perspectives. The first perspective considers the *proximal cause of the behavior* and requires that we examine both the role of external stimuli and internal neural states in prompting play behavior. Internal proximal causes of play such as "having fun" are assumed to be the product of evolution and imply that play is an adaptive behavior, but simply looking at the proximal cause of a behavior cannot illuminate how or why it may have evolved. The second perspective considers the life history of play (development of behavior during the process of maturation) and can be highly relevant to considerations of how juvenile play can produce adult benefits. The third perspective is perhaps the most crucial to evolutionary studies of play, as it seeks to understand the function of behavior. That play behaviors produce benefits that are indirect or delayed makes accurately assessing their function more difficult but also crucial to differentiating play from nonfunctional or dysfunctional behaviors. The fourth and final perspective addresses how a particular form of play evolved and can range from considering play as an exaptation of ancestral behaviors to putting particular forms of play in a phylogenetic context.

Evolution of Play in Nonhuman Animals

Although animals that play are relatively rare in all but a few taxonomic groups (such as primates, canids, cetaceans, parrots, and corvids), a diversity of play behavior has been observed across an intriguingly broad spectrum of animals. All three of the major forms of play (locomotor-rotational, object, and social) are prevalent; what is less clear is the degree to which nonhuman animals engage in various forms of play that require mental simulation (e.g., pretending, imagining, creative planning). Considering the diversity of play in animals can shed light on both the functional origins of play and the evolutionary processes that yielded species that play.

Examples of animal play. The sheer number of different kinds of play behavior that have been observed in animals highlights both the importance and heterogeneous nature of play. Although relatively few invertebrates play, a few notable exceptions are worth mentioning. Spiders of the species *Anelosimus studiosus* engage in nonconceptive "sexual play" that enhances the fitness of both male and female players (Pruitt et al. 2012). Among invertebrates, octopuses are the champion players, the subject of many anecdotal accounts of playful behavior in the wild. Captive studies have shown that when provided with objects constructed from Lego toys, most octopuses of the species *Octopus vulgaris* will play with the objects (Kuba et al. 2006). Many ethologists have been skeptical that invertebrates can display play behavior, but in both of these cases, the observed behavior met all five of Burghardt's play criteria, showing the value of employing objective play criteria to separate our anthropomorphic biases from our interpretation of behavioral observations.

Although birds and mammals are the most prolific animal players, other vertebrate lineages also display play behaviors. Cichlid fish have been observed to push around weighted thermometers in aquarium environments (Burghardt 2014). Many species of fish repeatedly leap over each other and also will bat around floating balls left in their enclosures (Burghardt 2005). Fagen (2017) has suggested that particular forms of salmon jumping should be considered play. Poison dart frogs engage in rough-and-tumble play, and tadpoles have been observed to ride the bubbles produced by aquarium aerators.

Play has also been observed in reptiles. Dinets (2015) reports that crocodilian species engage in locomotor play (mostly associated with riding currents or waves), object play (involving streams of water or floating objects), and even social play (giving each other rides, rough-and-tumble play with other species). Komodo dragons engage in object play that is reminiscent of domesticated dogs (Burghardt 2005). Some species of aquatic turtles will play in captivity with floating objects

and engage in tug-of-war bouts with their keepers (Burghardt 2005).

Many bird species engage in either locomotor, object, or social play with some orders (woodpeckers, parrots, songbirds, and raptors/pelicans) displaying all three kinds of play (Burghardt 2005). Many predatory birds engage in the playful dropping and re-catching of objects in midair. Aerial play is also common in birds, which will ride currents of air and perform acrobatics independent of any attempt to catch prey, avoid predators, or defend territory. Many birds play with various useless objects, which may aid in the development of later functional tool use and/or caching behavior. Social play is less common among birds, but two taxa – the parrots and the corvids – play together. Parrot species, which live in groups, initiate play-chases and play-fights (Diamond and Bond 2003). Ravens engage in social object play in which two individuals will play tug-of-war over a stick (Heinrich and Smolker in Bekoff and Byers 1998). Corvids and parrots possess a highly encephalized brain in comparison to other bird orders, suggesting a parallel with the most playful mammal species (Osvath et al. 2014). The playful nature of these species may also explain their exceptional ability to solve problems in both natural and laboratory settings (Bateson 2014).

Mammalian play is diverse, commonplace, and relatively well-studied. Marsupials play, with locomotor and social play being more common than object play. Kangaroos and wallabies engage in all three forms of play, including play-fighting, manipulation of found objects, and rapid-motion locomotor play (Watson in Bekoff and Byers 1998).

Play is even more common among the placental mammals. Pronghorn males join sparring matches that simulate actual fighting but mitigate the risks of real aggression (Miller and Byers in Bekoff and Byers 1998). Both wild and domesticated horses play as juveniles, running alone or in groups and sparring with others in their band (Cameron et al. 2008). Elephants play as juveniles and adults, both alone (manipulating objects, mud, dust, or water with tusks, trunk, mouth, or feet, or running/spinning/rocking/kicking) and socially (wrestling, sparring) (Lee and Moss 2014). Bears will wrestle and chase each other, manipulate objects, and play through locomotion and body rotation (Fagen and Fagen 2004). Mustelids are highly playful, primarily engaging in juvenile rough-and-tumble play that is crucial to the development of normal social behavior (Dallaire and Mason 2017).

As a marine mammal taxon, cetaceans demonstrate the great potential for play in aquatic environments (Paulos et al. 2010). Whale and dolphin locomotor-rotational play includes erratic swimming, aerial leaps/breaches/flips, intentional self-stranding, and surfing on waves. Object play is also common in both the wild and in captivity: bowhead whales play with floating logs, belugas and various dolphins play with bubbles they create, a variety of cetaceans play with both natural and human-made found objects, and orcas and a few other dolphin species have been observed playing with prey items. Cetacean social play in the water resembles social play in terrestrial mammals: young whales and dolphins are especially fond of chasing and bumping each other and performing aerial behaviors in synchrony. Another fascinating aspect of dolphin play is how often it includes other species, including birds, sea turtles, other cetaceans, and sea lions (Kuczaj and Eskelinen 2014).

The prominent role of play behavior in the development of primates has been appreciated for longer than in any other taxonomic group. This appreciation likely emerges from both how playful primates are and a certain degree of anthropomorphic interpretation of play behavior in other species. Every species of primate whose behavior has been marginally observed displays at least one type of play behavior (Burghardt 2005). The play of chimps and bonobos – our closest primate relatives – is of particular interest. Both chimps and bonobos engage in locomotor-rotational and object play, but social play is the most commonly observed form of play. Juvenile social play is similar in both species, but there is a marked difference in frequency and type of adult play: bonobo adults play more, perhaps because their social structures require more of the kind of social grooming and bonding that regular play can

provide (Palagi 2006). Some forms of bonobo play involve remarkable forms of risk and trust. Bonobos play the "ball game," a form of chase in which a male "leader" trusts his play partner to gently grasp his testicles while both circle around a tree or bush. Bonobos also play trust games such as the "hang game," in which one individual swings another by the arm from an elevated tree branch.

Rodents also play, although the distribution of rodent play is quite heterogeneous. Those rodents who do play tend to be social, and social play is the most commonly observed form of rodent play. Prairie dog adults facilitate social play with juveniles, and beavers "dance" together in their aquatic environment (Burghardt 2005). Rough-and-tumble social play is prominent in rat development, as juvenile rats attempt to gently bite their play partner on the neck, while that partner employs a variety of defensive tactics (Pellis and Iwaniuk 1999).

All canid species also play. Domesticated dogs are well-studied and represent an interesting case because they maintain strong social bonds with other dogs and with humans (Bekoff and Pierce 2009). The coevolution of humans and dogs may explain why domesticated dogs play more than their wild relatives: humans appear to have selected for neotenous traits that may extend juvenile behaviors into adulthood (Bradshaw et al. 2015). Dogs will run, jump, and manipulate objects in solitary play but are more likely to engage in a diversity of social play. Dogs play together through games of chase, play-fights, and mock sexual mounting (often in sex-reversed configurations). Dogs also enjoy social object play: "fetch" and "tug-of-war" are commonly played with humans, and dogs show increased interest in objects that other dogs or humans are manipulating (Bradshaw et al. 2015). The dog's enthusiasm for social object play has been exploited by breeders to create "sporting dogs" that will retrieve the quarry of human hunters (Sommerville et al. 2017).

Rules of the game. Social play is common among mammals, but there is some debate as to whether there are any universal features of mammalian social play. Animals playing socially may employ "play signals" that help their partners to differentiate between play and aggression. Bekoff and Pierce (2009) have suggested that these signals are part of a larger system of social rules that represent a definable animal morality. For example, individuals from various canid species appear to observe the following rules:

1. Signal that you want to play.
2. Employ real skills, but keep them in check.
3. Reverse roles.
4. Self-handicap.
5. Apologize if you break the rules.
6. Forgive rare transgressions.

Individuals who consistently break these rules are more likely to be socially ostracized, suggesting that canid play exists at least in part as a means of assessing potential social partners. Bekoff and Pierce (2009) emphasize that the rules of what's allowed in play may vary from species to species but that these general rules for playing are shared among many species that play socially.

Who plays, and when? Although there is increased appreciation and understanding of play behavior that occurs in adulthood, the vast majority of animal play occurs in juveniles (Burghardt 2014), a fact that strengthens the connection between development and play. Although there are no universal rules governing which sex plays or how, numerous studies have shown that sex matters in how individuals play; some studies have even demonstrated the different benefits that each sex realizes from playing (e.g., Dallaire and Mason 2017). In general, larger-brained mammal species tend to display more complex play behavior, although this correlation is stronger at higher taxonomic levels of comparison and may not distinguish more playful from less playful species within a clade (Iwaniuk et al. 2001).

Divergent, parallel, and convergent evolution of play. There are a great number of play behaviors across the animal kingdom that resemble each other in form, often sharing a common discernable function. How did evolutionary processes produce these similar behaviors? One possibility is that a common ancestor evolved a particular play behavior, passing this behavior

along to the many species that have since evolved. While this divergent explanation for animal play may apply to the very recent evolution of particular play behaviors in fine-scale taxonomic groups, it is clear that divergent evolution cannot explain the heterogeneous distribution of play behaviors across the tree of life. That the most prolific animal players are corvids, parrots, great apes, and dolphins demonstrates that some combination of convergent and parallel evolution must be responsible for the diversity of play we can observe (Osvath et al. 2014).

Distinguishing parallel from convergent evolution is difficult in general and may be particularly difficult for the various forms of play behavior. Parallel evolution suggests that evolved characteristics in a common ancestor served as a precursor trait that was subsequently similarly modified to produce similar play behaviors. Sociality may serve as such a precursor in many species, with social play evolving independently in related lineages but based upon shared foundational social interactions. The alternative is that play evolved convergently, with play behaviors evolving completely independent of each other, presumably due to similar environmental demands. Because play behaviors do not fossilize, it is very difficult to find evidence to untangle the subtle differences in pattern produced by convergent and parallel evolution (Burghardt 2005).

Phylogenies of play. One way to determine how play has evolved is to place different kinds of play behaviors on the tree of life, looking for patterns that would be indicative of convergent, parallel, or divergent evolution. Where play is less common, the power of convergent evolution to independently produce play behavior in disparate lineages is clear. If spiders and octopuses are the only invertebrates yet known to play, it is highly unlikely that these behaviors were inherited from a common ancestor (divergent evolution) or even emerged from the independent modification of traits inherited from a common ancestor (parallel evolution). Interestingly, in birds it also appears that the two major taxa that are the most prolific social players – corvids and parrots – are most likely to have independently evolved their similar forms of social play, as both have many closer relatives that do not play socially (Diamond and Bond 2003).

While octopuses, corvids, and parrots may have each evolved play independently *as lineages*, play is common among species within each of these clades, suggesting that divergent evolution may explain the distribution of play at lower taxonomic levels. The most compelling case for divergent evolution of play occurs in particular mammal lineages. All primate species and all canid species play, suggesting that the common ancestor of each of these clades displayed some form of play behavior. Play is also sufficiently common among placental mammals (Burghardt 2005) that it is reasonable to surmise that the common ancestor of all mammals may have displayed play behavior, although the finding that brain size correlates more strongly with play between rather than within clades suggests a role for parallel evolution of mammalian play (Iwaniuk et al. 2001). A study of play among the muroid rodents revealed that neither divergent nor convergent evolution provided a satisfactory explanation of the heterogeneous level of play among species in the clade, suggesting a role for parallel evolution of play (Pellis and Iwaniuk 1999).

Evolution of Play in Humans

Our interest in the play of other animals likely stems from our desire to understand our own very playful nature. Human play has many products that can be readily observed in both small-scale and large-scale societies. Musical play and dance are a nearly ubiquitous feature of human societies. Every culture has its own kinds of games and sports. Word play, jokes, and other creative uses of language suggest that words aren't just for functional communication. While art may be a very serious business in particular segments of many human societies, our drive to playfully create appears to be as ancient as the cave paintings of Chauvet or Maros.

Play in human juveniles. Children are prolific players. The incredible diversity of what constitutes a "toy" (and the broad range of target

ages for toy designs) underscores the importance of object play to young humans, but kids are also highly adept at turning all manner of found items into play objects. Locomotor-rotational play emerges within the first year of life and is a whole-body experience: infants move their limbs, use their hands to grasp, and explore with their mouths. Playground equipment is designed to meet the play demands of older children for climbing, sliding, swinging by their arms, and moving rhythmically. Children also demonstrate from an early age the importance of mental play to humans, eventually becoming immersed in a world of imaginative play that can be – from their perspective – indistinguishable from experienced reality.

What makes locomotor-rotational, object, and imaginative play in human children all the more fascinating is how often these forms of play are also social. Children love to play games with both adults and other children that involve chasing and mimicking movement. All manner of objects are used to play with others. And imaginative play frequently involves the creation of fantasy worlds and detailed role-play with other children.

A particularly well-studied form of social play in human juveniles is rough-and-tumble play. As with forms of rough-and-tumble play displayed by other animals, children will initiate bouts of vigorous but also restrained hitting, pushing, and wrestling, with larger children self-handicapping to maintain a playful interaction. Many studies have demonstrated the gendered nature of this sort of play: boys are far more likely than girls to engage in rough-and-tumble play. While many have suggested that these differences emerge from sex differences in hormonal expression, it is very difficult to separate out the effects of cultural expectations on the relative prevalence of rough-and-tumble play in girls and boys. Future work is needed to assess how gender expectations and biological sex interact developmentally to produce rough-and-tumble play.

Developmental role of play. Play is an essential component of normal human development. Children are playful from an early age; some have suggested that the rolling, punching, and kicking that occur in utero are the first forms of play to emerge (Brown 2009). A few months following birth, human infants begin a process called attunement, an interactive form of play that both strengthens the parent-offspring bond and builds cognitive skills. In their first year, infants also engage in a wide variety of locomotor-rotational play, allowing them to develop the physical coordination, strength, and balance required to begin walking upright. Objects also play an important role in early childhood, as manipulating various components of the encountered environment fosters understanding of physical properties.

A major transition from infancy into early and middle childhood occurs when children move from playing strictly with adults or older children to playing socially with their peers. While locomotor play and object play still allow for development of physical aptitudes and understanding, childhood shifts dramatically toward fostering an understanding of how to interact with other individuals. Children's social play can be seen as a way of building two fundamental understandings, a general awareness of how other humans respond emotionally to various kinds of interactions and a more specific awareness of the cultural rules that govern their particular society. The cultures in which children develop vary dramatically, but the role of social play in familiarizing children with the norms of those cultures is invariant.

Adolescence is a period of development with radically different meaning in different human societies. In some societies – particularly smaller-scale subsistence societies – adolescence may be a time in which children assume adult roles (this is especially true of girls). In large-scale societies that require huge amounts of learning in order to attain sociocultural maturity, functional adolescence may extend well beyond the attainment of physical and reproductive maturity. While adolescence varies in timing and duration, it does have some common features across cultures. There are shifts in social play from modes that emphasize group dynamics (such as friendship alliances) to modes that emphasize courting and mating behaviors. It could be argued that where "dating" behavior occurs, adolescents are essentially playing at mate selection and pair

bonding in preparation for adulthood. Another key aspect of play in adolescent development relates to experimentation with ideas outside of the family: adolescents become open to new and foreign experiences that have the potential to dramatically broaden their cultural repertoire.

Humans are the ultimate neotenous species: we maintain juvenile characteristics for a very large fraction of our overall lifetime. Long periods of childhood and adolescence allow for the advanced development of a variety of physical skills (such as throwing, chasing, running, and fighting) that may have been crucial to the survival of our ancestors. This extended maturation process also increases our ability to learn culturally and may account for our success not only relative to other primates but also relative to other (now-extinct) hominin species (Nowell 2016). Play is a very effective means by which the long developmental period of human juveniles can be leveraged to maximize behavioral plasticity in relation to a variable environment (Pellegrini 2009).

Play in human adults. The degree to which human adults play is a matter of some debate, as many forms of adult play behavior are intertwined with rigid rules, competition, and social/sexual signaling. Still, some have argued that adult play is a key expression of personality (Brown 2009). Humans are a species capable of lifelong learning, which means that some forms of play could continue to serve the same developmental roles that dominate childhood and adolescence. The role of play in adult tinkering, experimenting, and discovery is well-studied (Bateson 2014), but other play-like behaviors displayed by adults merit further investigation aimed at determining if adults frequently use play in ways that are analogous to the play of children and adolescents.

Many functional roles of human play. Play behavior serves many functional roles in humans. Some of these functions are directly analogous to the functional roles of play in other animals. A young child climbing on a playground structure is developing locomotor skills and potentially training for the unexpected. Humans playing around with tools to make things or trying out various sports are assessing their physical and cognitive capabilities. Forms of social play ranging from dancing to board games to competitive sports all open up the opportunity to assess the reliability and capabilities of potential social partners. A child playing by the rules of a recess kickball game is learning both social norms for fair play and how to cooperate with classmates.

Clearly there is a continuum between the play of other animals and human play, but the functional role of play in humans appears to be different in both extent and kind. Self-assessment provides one example of an "extended function" of human play. Whereas other animals may use self-assessment to determine what prey are profitable to pursue or to what degree they stand a chance in direct forms of sexual competition, humans actually use play to self-assess and decide what skills to work on for a lifetime. This decision may not be conscious: we find playing at things that bring us success to be more rewarding, which means that we are more likely to pursue and practice those activities which we experience as "fun." Studies have demonstrated the level of mastery that can emerge from this kind of autotelic play behavior. For example, rugby players are dramatically better at distinguishing between deceptive and honest body movement signals.

The extent of human social play also exceeds that of other animals. This extension of social play probably is a reflection of the degree to which humans rely on cooperation with nonrelatives. Other animals may use play to choose allies from within a small social group, but human play forms such as joking, dancing, game playing, sports, and playful conversation are used to create an extensive network of friends that engage in mutual aid. Play's potential to foster social cohesion may have reached its apex in humans.

Another clear extension of human play relates to when humans play throughout their life histories. While juveniles may play differently than adults, humans tend to play in multiple ways throughout their lives. Play can be used to develop new skills at any age, and humans stay motivated to play throughout adulthood and even as they senesce. While physical forms of play may decrease in frequency as humans age, other forms of play – such as language play or creative play – may be maintained or become more frequent.

While most play by adults in other animals is directed at juveniles (and thus may be related to "parenting for play"), human adults also engage in extensive play with other adults.

In nonhuman animals and in smaller-scale human societies, play is generally not needed in order to "keep in shape": the day-to-day activities required to meet basic needs maintain physical fitness. Humans have clearly evolved a "use it or lose it" physiology that adjusts both musculature and cardiopulmonary capacity to whatever level of physical activity has been recently undertaken. In large-scale industrialized societies, meeting basic needs through various economic exchanges often does not require much physical exertion. In these societies, play has taken on a new role as a means of maintaining physical fitness. While not all forms of human exercise is playful – for most people, running on a treadmill is work! – many forms of play have assumed a role in producing optimal health outcomes.

Perhaps the most distinctive function of play in humans is our use of mental play. Humans have a strong ability to play entirely in our own minds. One such form of play involves simulation of fantasy worlds via mental rehearsal or reenactment, which allows us to both process past events (Dallaire et al. 2017) and to plan and prepare for future events. In this sense, fantasy play is a kind of time travel, allowing us to learn from things that have already happened and to anticipate events that haven't yet happened. Mental play can also be used to come up with new cultural ideas. In humans, imagination and improvisation are closely related to problem-solving and innovation; our creativity relies in large part on our playfulness (Bateson 2014). We like to play with ideas that we have learned from others, tweaking and modifying existing culture in a way that allows for collective innovation through cumulative culture. It is hard to know if other animals engage in mental play, and there are a few other species (such as ravens) that appear to come up with novel solutions to problems via playful behavior. But a consideration of the abundant cultural products of human mental play makes it clear that if we are not the only mental players, we certainly rely on mental play to an unprecedented extent.

One interesting aspect of human play behaviors is that many lead to what would be best categorized as performance. In animals, the difference between play and performance is generally pretty clear: playing at mock-mating happens at a different developmental stage and in a different context than real mating, and there is a distinct behavioral difference between play-fighting and agonistic fighting. But many human behaviors that relate to play blur the line between true play and behaviors with a more immediate function. A musician may be "playing" music (and certainly a lot of music-making is playful), but this playing could be a display with the potential to attract a mate. Is the cultural importance of music the result of selection for play itself or a product of sexual selection? The fluidity of human play makes answering such a question difficult. An athlete may be playing a particular team sport, but this playing could be a display with the potential to cement cooperative relationships with other players once they leave the field of play. The manner in which play is integrated into everyday human life (and not just among children) makes it difficult to distinguish true play from play-like behaviors co-opted to produce immediate benefits.

The Playful Mind: Implications for Human Well-Being

That play is an evolved behavior has important implications for human health and well-being. It is clear that play is an adaptation that empowers complex learning, mental preparation, physical fitness, social bonding and cooperation, and discovery and creation. We are in many ways a species that depends on play, which means that maintaining access to beneficial opportunities to play is a serious health issue.

Play as a cause and correlate of mental health. There has been a long debate in the animal behavior and psychology literature about whether or not play can be used as either indicative of welfare or as a means to achieving optimal

welfare. Many studies have shown that play can improve the welfare of both animals (e.g., Held and Špinka 2011; Bateson 2014) and humans (Landreth 2002). A more subtle question is whether the presence or absence of play behavior can be used to assess welfare. While there is compelling evidence that depression of play activity can be used as an indicator of poor welfare, the opposite is not true: an abundance of play does not necessarily indicate positive mental or physical health (Dallaire et al. 2017). This is particularly true in humans, who may use forms of solitary play, such as reenactment, to deal with trauma. An exciting possibility is that shifts in the mode of play – such as from social to solitary – might be used to diagnose the affective state and overall welfare of human patients.

Zone of proximal development and productive forms of play. Russian psychiatrist and researcher Lev S. Vygotsky was the first to conceptualize the idea of a *zone of proximal development* (ZPD). The ZPD was based on the idea that in order to gain new understandings, a learner must be challenged beyond their current level of competency but not be overwhelmed by a challenge far beyond their capabilities. Play often appears to occur in environments that seem to create a ZPD: we don't enjoy playing in environments that present too few challenges because they are boring, but we also don't enjoy playing in environments that are overly challenging because they are unduly stressful. Vygotsky saw play as the ideal means by which children productively enter the ZPD and orchestrate their own learning. The kind of play that Vygotsky's research demonstrated was key to learning is observed less in children today than those of past generations, suggesting a unique challenge to modern-day educators: how do we restore play as an optimal means for enabling learners to enter their ZPD (Bodrova and Leong 2015)?

Changes in the role of play in large-scale societies. Large-scale, industrialized societies have dramatically changed what we play, how we play, and how much we play at different points in our life histories. If a "relaxed field" is required to stimulate play behavior, industrialized societies certainly increase the abundance of such environments: compared to our ancestors, a much larger fraction of people are free from daily concerns about food availability or personal safety. An overall increase in leisure time also enables many people more time in which to play in this relaxed field. In addition to creating an environment that is conducive to play, large-scale societies tend to require more extensive cultural learning; this requirement for extended and sometimes lifelong learning can functionally extend adolescence (a time of intense play) and make play important throughout adulthood.

Cultural evolution has also dramatically changed how we play. The Internet creates the potential for social interaction that differs from our ancestral social environments in both extent and kind, opening up unprecedented opportunities for social play. Virtual online worlds become not just additional spaces in which to play: they create entirely new play environments. Industrialized societies produce novel objects that foster totally new forms of play (e.g., skateboards, mountain bikes, skis, sailboats, and all manner of balls). Play has also been highly commercialized, opening up the possibility that forms of play behavior may be influenced not just by our evolved propensities to play but also by marketing.

Play has also infiltrated the world of design, where creative industries have strived to harness the power of play to create novel ideas and motivate extraordinary human effort. Companies provide their employees with break spaces that encourage play and try to incorporate play into the way that they address business challenges (Brown 2009). Although an understanding of our playful nature has impacted some workplaces, it would be mistaken to overestimate the extent of this impact: work environments that embrace play represent a tiny fraction of the overall global workplace and tend to exist in the sector of industries that rely on the creation of new products or other forms of novel design.

Play as a privilege. Although many people have been enabled to play more frequently and further into adulthood, this condition is far from universal. Inequities within and between societies create a dynamic in which some people live under ideal conditions for play and others are

deprived of the opportunity to play. This deprivation applies to children as well as adults: kids who are undernourished or have to work are less likely to spend their time playing (Bateson 2014). Acknowledging that play is currently a privilege but is also an evolved developmental need, the United Nations issued a proclamation establishing play and a "universal and inalienable right of childhood" (Landreth 2002).

Mismatch theory and modern play. Human play behaviors evolved in a very different environment than the one that most people experience today. Our play emerged in smaller social groups of hunter-gatherers who interacted with far fewer individuals during a human lifetime and maintained a much smaller base of material culture. Thanks to the prolific cultural evolution produced by modern industrialized societies, we now have access to far more objects to play with, environments to navigate, and people with whom to interact. The cultural evolution that creates these new environments dramatically outpaces human genetic evolution, setting up the potential for play behaviors that are "mismatched" to our current environment.

One potential outcome of this mismatch is various forms of play-related addictions. Perhaps the most obvious play addictions are to electronic games, particularly those which combine vivid forms of fantasy play with real-time social interactions with a limitless supply of play partners (Brown 2009). Many forms of gambling may also exploit playful human curiosity, leading some people to become compulsive gamblers. Such addictions can, ironically, pull people away from healthy forms of play that are key to maintaining physical and mental health.

Another potential outcome of this mismatch is play that is excessively risky. Again, it is the use of new cultural technologies that may shift normal play behavior into maladaptive territory. Online dating apps may turn normal sexual play into a compulsion. Access to various kinds of motor vehicles produces new and dangerous forms of locomotor play that can be a major source of mortality among young adults. Certain forms of "new play" enabled by both novel material culture and novel cultural ideas (such as free solo rock climbing, big wave surfing, and BASE wingsuit jumping) attract some people to play under extraordinarily risky conditions.

Understanding how and why humans evolved to play can enable us to better design modern societies – and forms of play within those societies – that create fewer of these pathologies and extreme risks.

Conclusion

Play is a prevalent animal behavior that appears to be an adaptation to the challenges of a dynamic social and ecological environment. The role of play is most prevalent in juveniles, with many of the benefits of play being manifested through developmental processes, but play can also serve a function in adulthood. While the most complex forms of play are found in the mammalian lineage, the prevalence of play in other animal groups suggests both its broad adaptive utility and the role of play in the success of many lineages of the animal kingdom.

The delayed nature of play benefits, combined with the difficulties of comprehensively observing any complex animal behavior in a natural setting, makes studying play from an evolutionary perspective a challenge. There is still much scientific work to be done to unravel the functions of play in both humans and nonhuman animals and to illuminate how play evolved. A major innovation in the field has been the positing of clear, distinct hypotheses that make contrasting predictions about what we should observe in animals that display play behavior.

Humans are a particularly playful species, with play behavior enabling much of the learning that occurs during humans' extended developmental period. The persistence of play well into adulthood suggests that human neurological development continues well past attainment of sexual maturity and that in some ways humans may be continually developing. Understanding humans as a species that evolved to develop via play can enable us to design better educational systems, improve workplace creativity, and foster better mental and physical health outcomes.

Cross-References

- Combat Sport
- Development of Adaptations
- Dominance in Humans
- Duration of Childhood
- Empathy in Rats
- Evolution of Fighting Assessment Abilities
- Language Acquisition in Infants and Toddlers
- Learning versus Imitation
- Marc Bekoff
- Newborn Behavior
- Peer Socialization
- Play and Social Learning
- Play and Tool Use
- Play Fighting in Boys
- Proto-tool
- Sensorimotor Play
- Social Play
- Social Withdrawal in Childhood
- Tool Play

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